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Originals

Structure and Affinities of the Petrified Plants from the Cretaceous of Northern Japan and Saghalien X

Two *Sequoia*-like Cones from the Upper Cretaceous of Hokkaido

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北日本及びサハリンの白亜紀産石化植物 X

北海道白亜紀産の二つのセコイア様球果

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A taxodiaceous seed cone from the Upper Cretaceous of Haboro, Hokkaido, is described as a new genus, *Haborosequoia,* based on anatomical features. Vascular strands to the bract and scale in *Haborosequoia* show a very similar pattern to those in *Sequoia, Sequoiadendron* and *Metasequoia*. *Haborosequoia* differs from the latter three in the external morphology of the bract-scale complex and the resin-canal arrangement. Another *Sequoia*-like cone from the Upper Cretaceous of Obira, Hokkaido closely resembles *Sequoia* and *Sequoiadendron* in gross morphology.

(Continued from Ohsawa et al., Phytogeogr. Taxon **39**: 97–105, 1991)

Introduction

Studies on taxodiaceous seed cones from the Cretaceous of Japan were started by Stopes and Fujii (1910) who described *Cunninghamiostrobus yubariense* Stopes et Fujii from the Upper Cretaceous of Hokkaido. Recently, we have described *Yezosequoia shimanukii* Nishida et al. (1991), *Parataiwania nihonghii* Nishida et al. (1992), and *Sciadopitys yezo-koshizakae* Ohsawa et al. (1992). This paper is our fourth report on taxodiaceous seed cones from the Upper Cretaceous of Hokkaido; it describes two kinds of cones.

Materials and methods

Specimen no. 890715 is a well-preserved fossil seed cone collected by Mr. Isamu Nakajima from the riverbed of the River Machiyoizawa, a tributary of the River Haboro, Haboro Town, Rumoe-gun, Hokkaido. The fossil cone is embedded in a nodule containing an ammonite, *Hyphantoceras oshimai* and the age is estimated as Santonian (personal communication, Dr. Ikuo Obata).

Specimen no. 888207 was collected by Mr. Toshio Shimanuki as a nodule from the riverbed of the River Kamikinenbetsu, a tributary of the River Obirashibe, Tappu, Obira Town, Rumoegun. The fossil-bearing nodule originates from the Uppermost part of the Middle Yezo Group to the Maine part of the Upper Yezo Group sediments which are widely distributed in the upper reaches of the River Kamikinenbetsu and are dated as Turonian to Santonian (Tsushima et al. 1958, Matsumoto et al. 1976). This fossil cone is poorly preserved so we could not examine its detailed histology and cannot describe it as a new species. All micropreparations were made by the ordinary peel technique using 1.8% hydrochloric acid as an etching reagent.

Systematic treatment

Order Coniferales

Family Taxodiaceae

Genus *Haborosequoia,* gen. nov.

Type species *Haborosequoia nakajimae* sp. nov.

Diagnosis of Genus. Coniferous seed cone ovoid, consisting of more than 15 helically-arranged bract-scale complexes. Bract and scale fused completely to build cuneately-peltate bract-scale complex lacking horizontal groove on distal surface. Pith of cone axis composed of thin-walled parenchyma. Vascular cylinder of cone axis composed mostly of secondary xylem; primary xylem endarch. Cortex composed of parenchyma, lacking resin canal. Single cylindrical vascular trace to bract-scale complex dividing repeatedly to form two horizontal rows of vascular strands in middle area of bract-scale complex. Several blind resin canals in bract-scale complex, branching to form numerous resin canals arranged mainly in irregular rows on abaxial side of complex. Fundamental tissue of complex composed of parenchyma and fibers.

Etymology. Genus name, *Haborosequoia,* means *Sequoia* from Haboro, type locality.

Diagnosis of species. As for Genus.

Type and deposition. No. 890715 (holotype) deposited in Laboratory of Phylogenetic Botany, Faculty of Science, Chiba University.

Locality. Machiyoizawa, a tributary of the River Haboro, Haboro, Hokkaido.

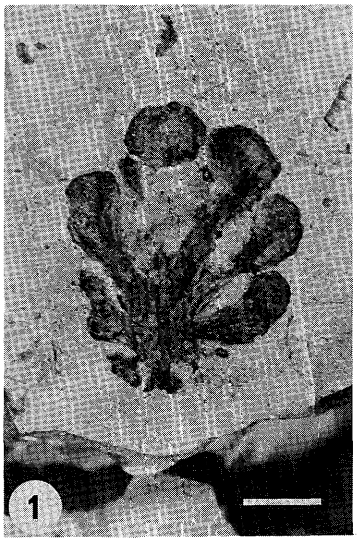
Horizon. Upper Yezo Group; Santonian, estimated by *Hyphantoceras oshimai.*

Etymology. Specific epithet dedicated to Mr. Isamu Nakajima, Mikasa City, Hokkaido, specimen collector.

Cone structure. The seed cone is ovoid, 16–17 mm high and 14–15 mm in maximum diameter (Fig. 1). More than 15 bract-scale complexes are arranged helically on the cone axis (Figs. 1, 7). They are cuneately peltate, 6–8 mm long, 4.5–6 mm wide and 2.5–3.5 mm thick, lacking a horizontal groove on the distal surface (Fig. 2). The bract and scale are completely fused and indistinguishable externally (Fig. 2).

Cone axis. The cone axis is 2.4 mm in diameter (Fig. 3). The pith is 0.6–0.8 mm in diameter and composed of thin-walled parenchyma cells that are elongated vertically, 10–24 μm in diameter and 26–66 μm in length (Fig. 4). The vascular cylinder is 0.4–0.6 mm thick, 1.4–1.6 mm in diameter and composed mostly of secondary xylem. Secondary xylem tracheids are 10–16 μm in diameter. Endarch primary xylem strands are visible at the inner edge of the vascular cylinder (Fig. 4). Rays are uniseriate and usually 1 to 3, rarely up to 5 cells high (Fig. 5).

The cortex is 0.3–0.6 mm thick and composed of parenchyma cells that are 16–36 μm in diameter and 60–120 μm in length, and scattered elongated sclerenchyma cells, 24–60 μm in diameter with walls 10–24 μm thick (Fig. 6).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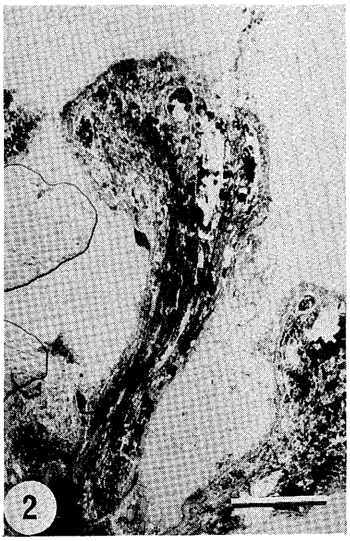
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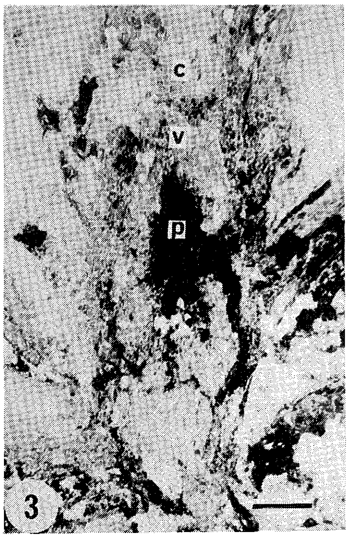
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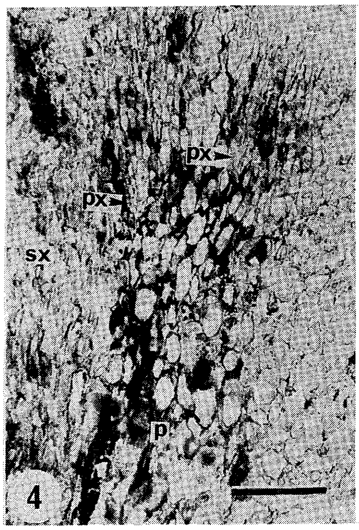
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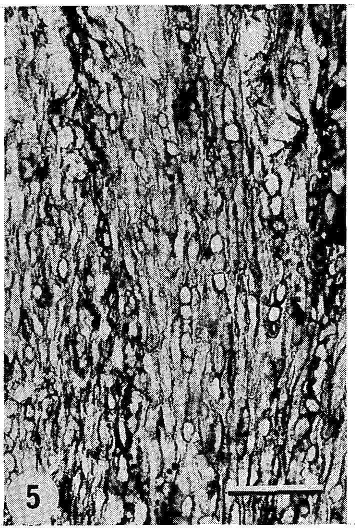
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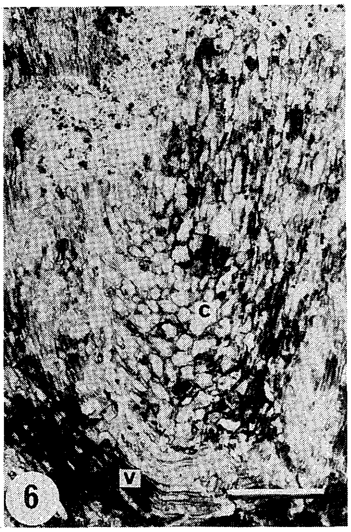
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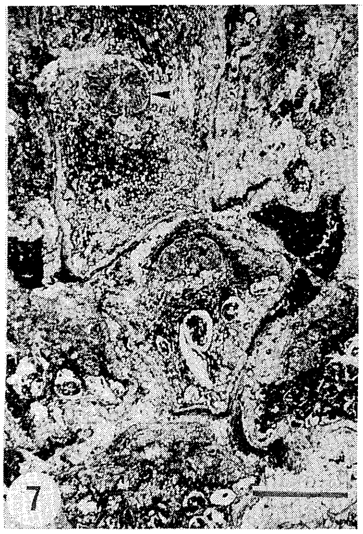
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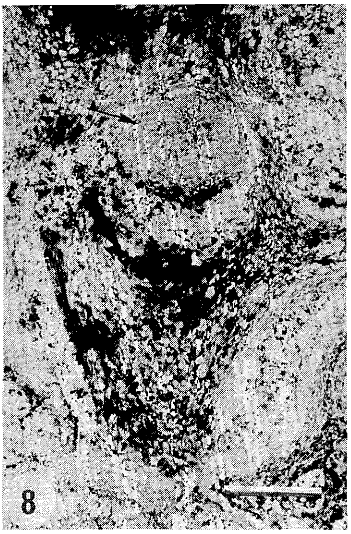
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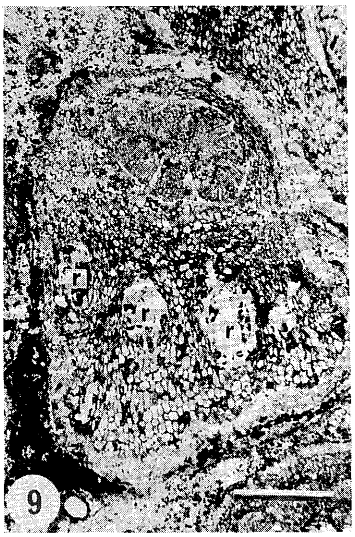
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There are no resin canals in the cortex. The hypodermal and epidermal layers of the cone axis are not preserved.

Bract-scale complex. A vascular trace supplying the bract-scale complex diverges from the vascular cylinder of the cone axis as a cylindrical unit with oval cross section (Figs. 7, 8). A small abaxial part of the vascular trace separates first (Figs. 10, 18B). The remaining horseshoe-shaped strand extends laterally and divide several times to form 18 to 20 vascular strands arranged in two horizontal rows (Figs. 11, 12, 13, 16, 18). The phloem of the vascular strands in the adaxial row face the adaxial side and those in the abaxial row face the abaxial side. The vascular supplies to the seeds branch from the strands in the adaxial row at the middle of the bract-scale complex (Fig. 15).

There is no resin canal at the basal-most part of the bract-scale complex (Fig. 8). However, several blind resin canals appear in the basal part of the bract-scale complex (Fig. 9). They divide and several new blind canals appear to form 15 to 20 resin canals arranged in two or three irregular-horizontal rows at the abaxial side of the middle of the complex (Figs. 11, 12, 18). Some of the lateral canals bend around the lateral side of the vascular bundles and enter the adaxial side at the distal part of the complex (Fig. 13). The resin canals are large, 200–416 μm in diameter in the basal-to-middle part, 320–720 μm in diameter at the abaxial side of the distal part and 160–400 μm in diameter at the adaxial side of the distal part.

The fundamental tissue of the bract-scale complex consists of parenchyma and scattered fibers (Figs. 14, 16, 17). The parenchyma cells are polygonal in transverse section and 22–70 μm in diameter. The fibers are round or polygonal in transverse outline and 30–80 μm in diameter with walls 14–30 μm thick. They are scarce in the base and abundant in the distal part of the complex. The hypodermis is composed of two to five layers of thin-walled parenchyma cells (Figs. 16, 17). The epidermis of the adaxial and lateral sides of the distal part of the complex has short trichomes (Fig. 17).

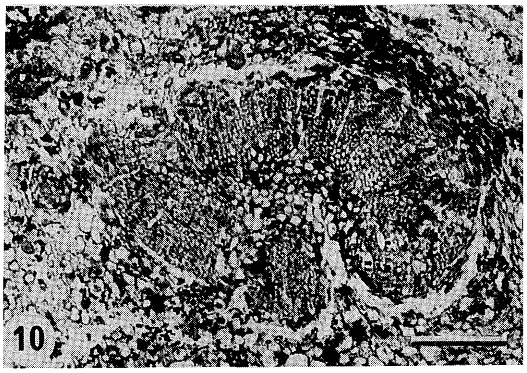
The seeds are not preserved but were probably inverted judging from the behavior of the vascular supplies.

Affinity. As described above, *Haborosequoia nakajimae* shows affinities with *Sequoia*, *Sequoiadendron* and *Metasequoia,* because they share peltate or cuneately-peltate bract-scale complexes consisting of an equal-sized completely fused bract and scale, cylindrical vascular traces to the complex, and more or less the same size and number of vascular strands in the bract and scale (LaPasha and Miller 1981, Nishida et al. 1991).

However, *Haborosequoia nakajimae,* differs from *Metasequoia* in having helically-arranged instead of decussate bract-scale complexes. *Metasequoia* is also distinguished from *H. nakajimae* by having a abaxially-concave reniform vascular supply to the bract-scale complex (Table 1).

Sequoiadendron differs from *H. nakajimae* in having both abaxial and adaxial resin canals in the basal-to-middle area of the complex instead of only

Figs. 1–9. *Haborosequoia nakajimae,* gen. et sp. nov. 1. Longitudinal view of specimen embedded in sandstone nodule. Bar 5 mm. 2. Longitudinal section of cuneately-peltate bract-scale complex. Bar 2 mm. 3. Oblique section of cone axis showing pith (p), vascular cylinder (v), and cortex (c). Bar 2 mm. 4. Oblique section of cone axis showing pith (p), primary xylem strand (px), and secondary xylem of vascular cylinder. Bar 0.1 mm. 5. Tangential section of vascular cylinder showing uniseriate rays. Bar 0.1 mm. 6. Oblique section of cone axis showing vascular cylinder (v) and cortex (c). Bar 0.2 mm. 7. Cross section of basal part of bract-scale complexes supplied by cylindrical vascular trace (arrow). Bar 1 mm. 8. Cross section of basal-most part of bract-scale complex showing cylindrical vascular supply (arrow). No resin canals in this part. Bar 0.5 mm. 9. Cross section of basal part (slightly distal to fig. 8) of bract-scale complex showing resin canals (r). Bar 0.5 mm.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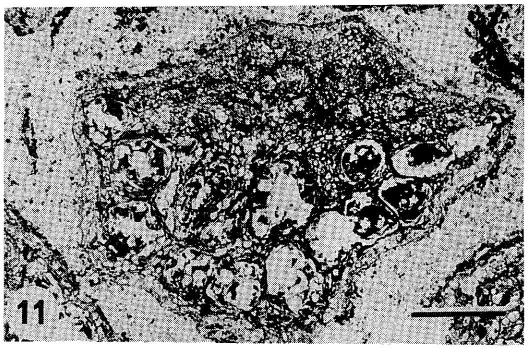
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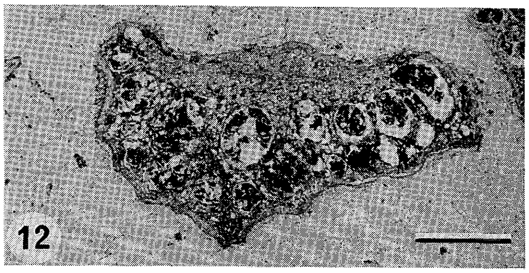
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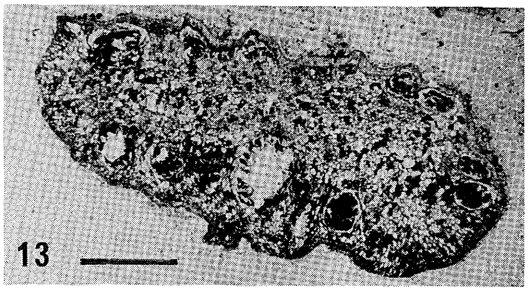
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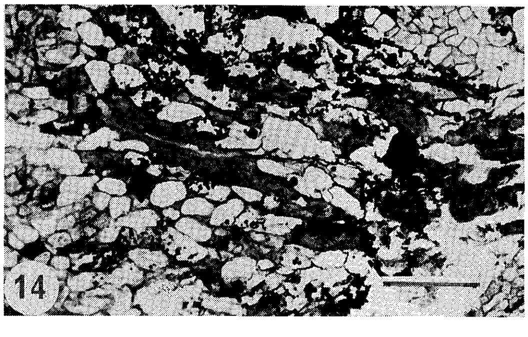
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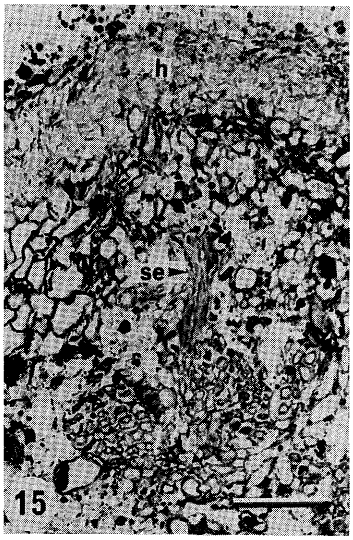
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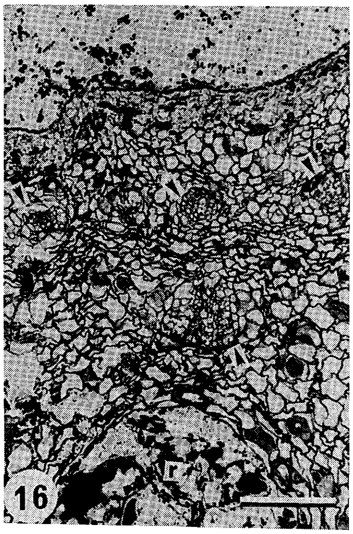
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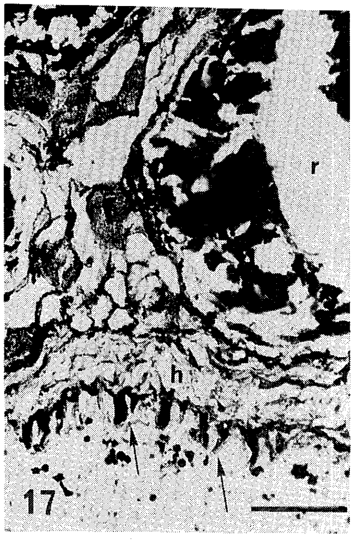
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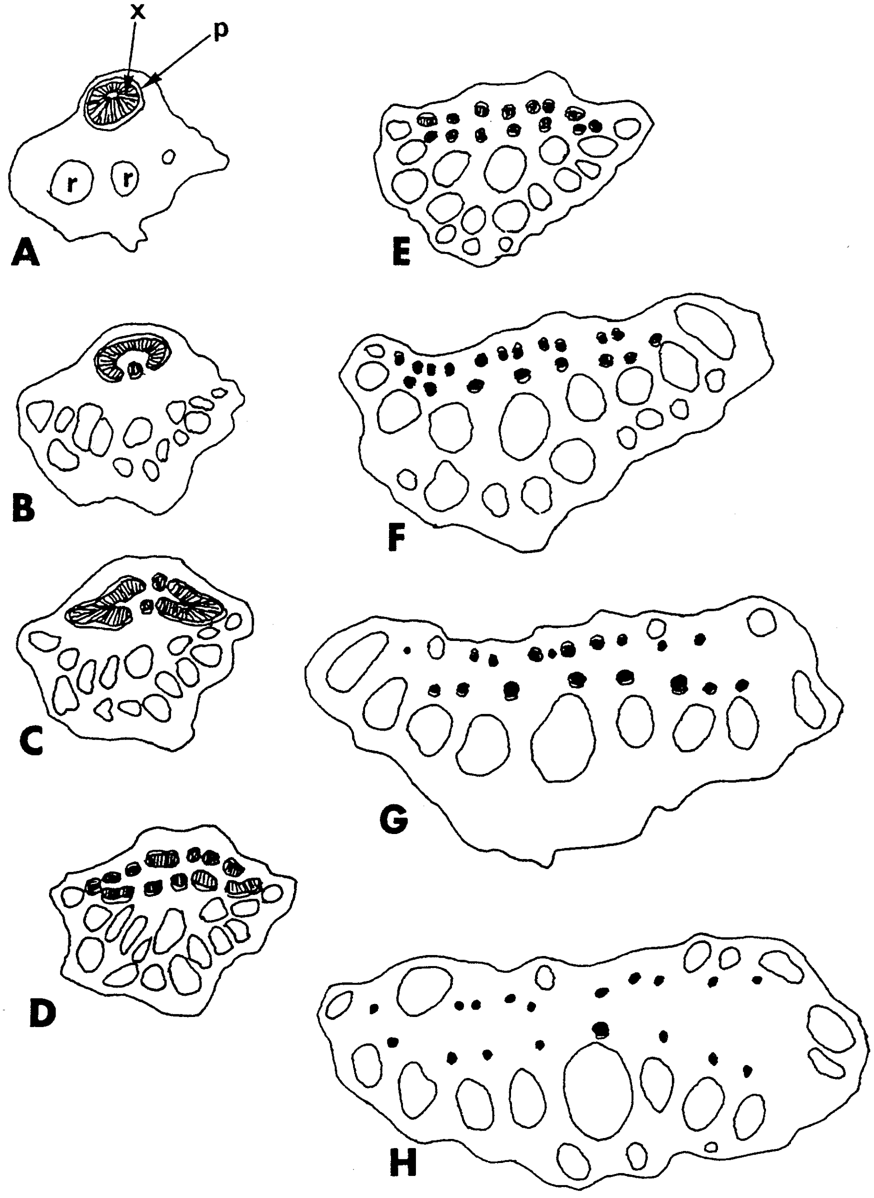


Fig. 18. Semi-diagrammatic figures of serial cross sections of bract-scale complex of *Haborosequoia nakajimae* showing arrangement of vascular bundles and resin canals. p: phloem, r: resin canal, x: xylem.

Figs. 10–17. *Haborosequoia nakajimae,* gen. et sp. nov. Cross section of base of bract-scale complex showing vascular supply to complex. Bar 0.2 mm. 11. Cross section of middle part of bract-scale complex showing arrangement of vascular strands and resin canals. Bar 0.5 mm. 12. Cross section of middle part of bract-scale complex showing arrangement of vascular strands and resin canals. Bar 1 mm. 13. Cross section of distal part of bract-scale complex showing arrangement of vascular strands and resin canals. Bar 1 mm. 14. Longitudinal section of bract-scale complex showing parenchyma and fibers. Bar 0.2 mm. 15. Cross section of middle part of bract-scale complex showing vascular trace to seed (se) and hypodermis (h) composed of thin-walled cells. Bar 0.1 mm. 16. Cross section of middle part of bract-scale complex showing vascular bundles arranged in two rows (arrows). r: resin canal at abaxial side of vascular bundles. Bar 0.2 mm. 17. Cross section of distal part of bract-scale complex showing trichome on epidermis (arrows). h: hypodermis, r: resin canal. Bar 0.1 mm.

Table 1. Comparison of diagnostic characteristics of bract-scale complex of *Haborosequoia nakajimae, Sequoia*-like cone from Hokkaido and related genera.

	External form and arrangement	Horizontal groove on distal surface	Form of vascular supply in basal part	Arrangement of vascular bundles in distal part	Arrangement of resin canals in middle part
Haborosequoia nakajimae gen. et sp. nov.	cuneately-peltate helical	absent	elliptical cylinder	adaxial side and median region	abaxial side; wide and numerous irregular 2–3 rows
Sequoia-like cone from Hokkaido	peltate helical	present	reniform cylinder	adaxial side and median region	present, but arrangement unknown
Austrosequoia wintonensis Peters et Christophel (1978)	peltate helical	present	not described	adaxial side and median region	abaxial and adaxial side;
*Sequoia sempervirens** (D. Don) Endlicher	peltate helical	present	elliptical cylinder	adaxial side and median region	abaxial side; mostly one row, two rows in central region
*Sequoiadendron giganteum** (Lindley) Buchholz	peltate helical	present	elliptical cylinder	adaxial side and median region	abaxial and adaxial side; both one row
*Metasequoia glyptostroboides*** Hu et Chen	peltate decussate	present	reniform cylinder	adaxial side and abaxial side	abaxial side single canal

*from Radais (1894) and Lemoine-Sebastian (1968). **from Sterling (1949) and our examination.

abaxial resin canals in the latter (Radais 1894, Lemoine-Sebastian 1968; Tab. 1). *H. namajimae* more closely resembles *Sequoia* than *Sequoiadendron* in these respects. However, *H. nakajimae* differs from *Sequoia* in having wider and more numerous resin canals in the bract-scale complex, and in lacking the horizontal groove of the cuneately peltate bract-scale complex (Tab. 1). The *Sequoia* group share horizontal grooves on the distal surface of the peltate bract-scale complex.

Some *Sequoia*-like cones have been described from the Cretaceous worldwide. *Austrosequoia wintonensis* Peters et Christophel (1978) from the Upper Cretaceous of Queensland, Australia closely resembles *Sequoia* and *Sequoiadendron* and has a horizontal groove on the distal surface of a peltate bract-scale complex. *Haborosequoia nakajimae* is distinguished from *Austrosequoia wintonensis* in having a cuneately peltate complex without a groove. Two species of *Nephrostrobus* LaPasha et Miller (1981) from the Upper Cretaceous of New Jersey, USA are also characterized by a peltate bract-scale complex, but differ from *H. nakajimae* in having a unique adaxially concave reniform arrangement of vascular strands in the transverse section of the complex. Thus, *H. nakajimae* is different from any known genera of the Taxodiaceae and should be a new genus exhibiting affinities with *Sequoia*-like allies.

A *Sequoia*-like cone

Specimen and deposition. No. 888207, deposited in Laboratory of Phylogenetic Botany, Faculty of Science, Chiba University.

Locality. Riverbed of River Kamikinenbetsu, Tappu, Obira Town, Hokkaido.

Horizon. Uppermost part of Middle Yezo Group to Main part of Upper Yezo Group, Turonian to Santonian.

Note. The cone is ellipsoid, 22 mm in height and 17 mm in maximum diameter (Fig. 19). More than 15 bract scale complexes are arranged helically on the cone axis. They are peltate and measure 4.5–6.5 mm long, 4–5.5 mm wide and 2.5–4 mm thick with a horizontal groove on distal surface (Figs. 19, 22). The bract and scale are completely fused.

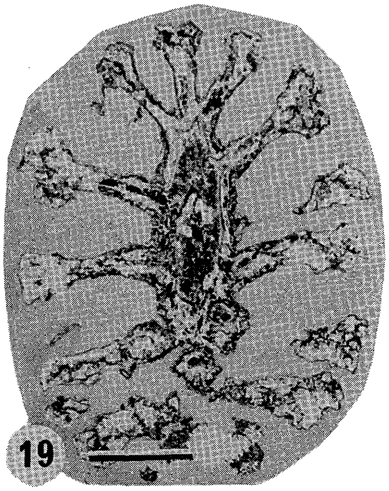
Cone axis is 4–4.5 mm in diameter; the pith is 1.3 mm in diameter. The vascular cylinder is 0.5–0.9 mm thick, 2.8 mm in diameter and composed mostly of secondary xylem. The cortex is 0.6–0.8 mm thick.

The vascular trace to the bract scale complex diverges from the vascular cylinder of the cone axis as a cylindrical unit which in reniform in cross section (Fig. 20). The vascular trace divides and extends laterally to form 15 to 16 vascular strands arranged in two horizontal rows (Figs. 21, 23, 24, 25, 26). The phloem of the adaxial strands face the adaxial side and those of the abaxial strands face the abaxial side. Resin canals were not seen in the basal-to-middle areas of the complex because of poor preservation but a few resin canals can be seen in the distal area.

The fundamental tissue of the bract-scale complex is parenchyma and scattered fibers (Fig. 21). Parenchyma cells are 16–60 μm in diameter and the fibers are 26–80 μm in diameter with walls 8–20 μm thick. The hypodermis is composed of two or three layers of thin walled cells.

No seeds are preserved.

Affinity. As mentioned above, the cone closely resembles *Sequoia, Sequoiadendron* and *Metasequoia* in gross morphology, especially in having peltate bract-scale complexes with a horizontal groove on distal surface, cylindrical traces to the bract-scale complex, and the vascular traces in the bract and scale that are more or less the same size and number (LaPasha and Miller 1981, Nishida et al. 1991). However, bract traces of *Metasequoia* enter the abaxial side of bract-scale complex except for central strands that enter to the middle horizontal groove region (Sterling 1949). In this specimen as well as *Sequoia* and *Sequoiadendron,* all the bract traces enter the middle horizontal groove region (Radais 1894). The specimen also differs from *Metasequoia* and resembles *Sequoia* and *Sequoiadendron* in having helically arranged bract-scale complexes (Tab. 1). Although this specimen closely resembles *Sequoia* and *Sequoiadendron,* it differs from them in having an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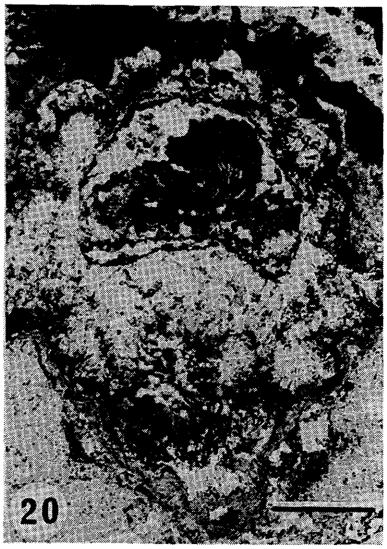
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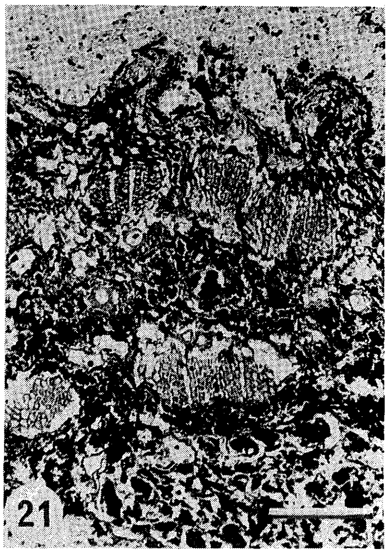
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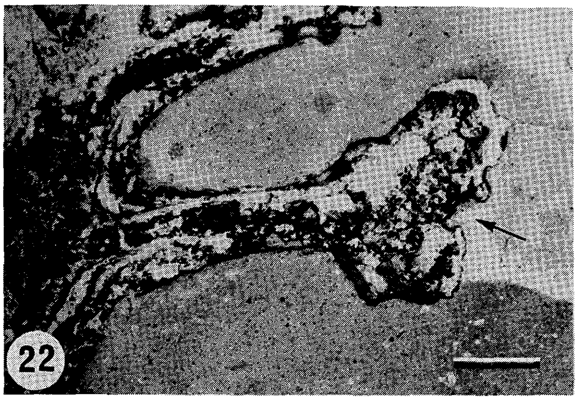
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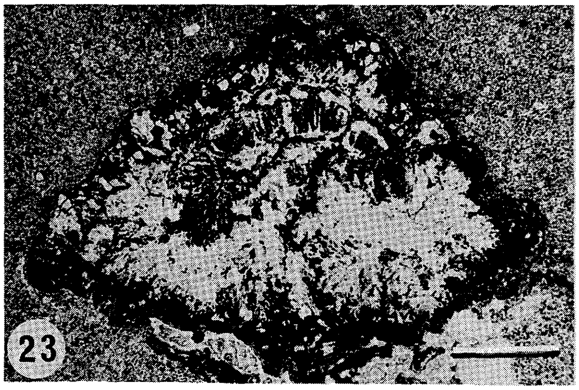
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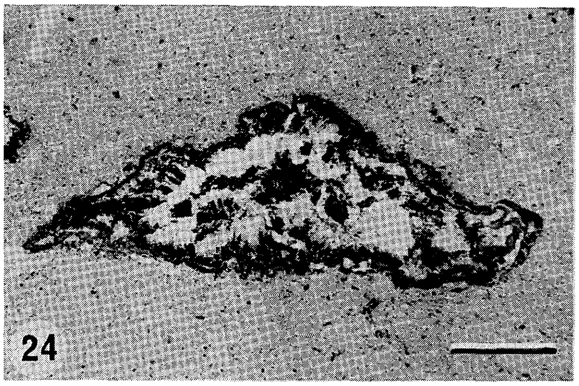
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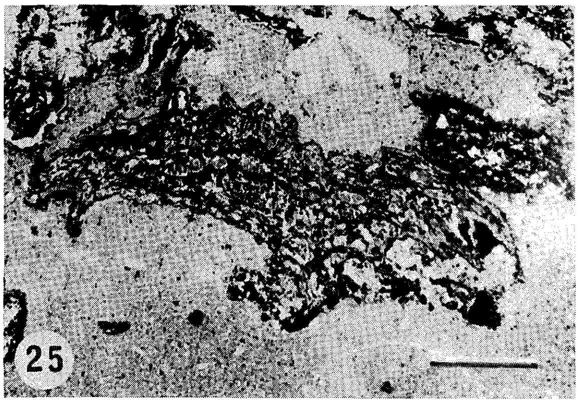
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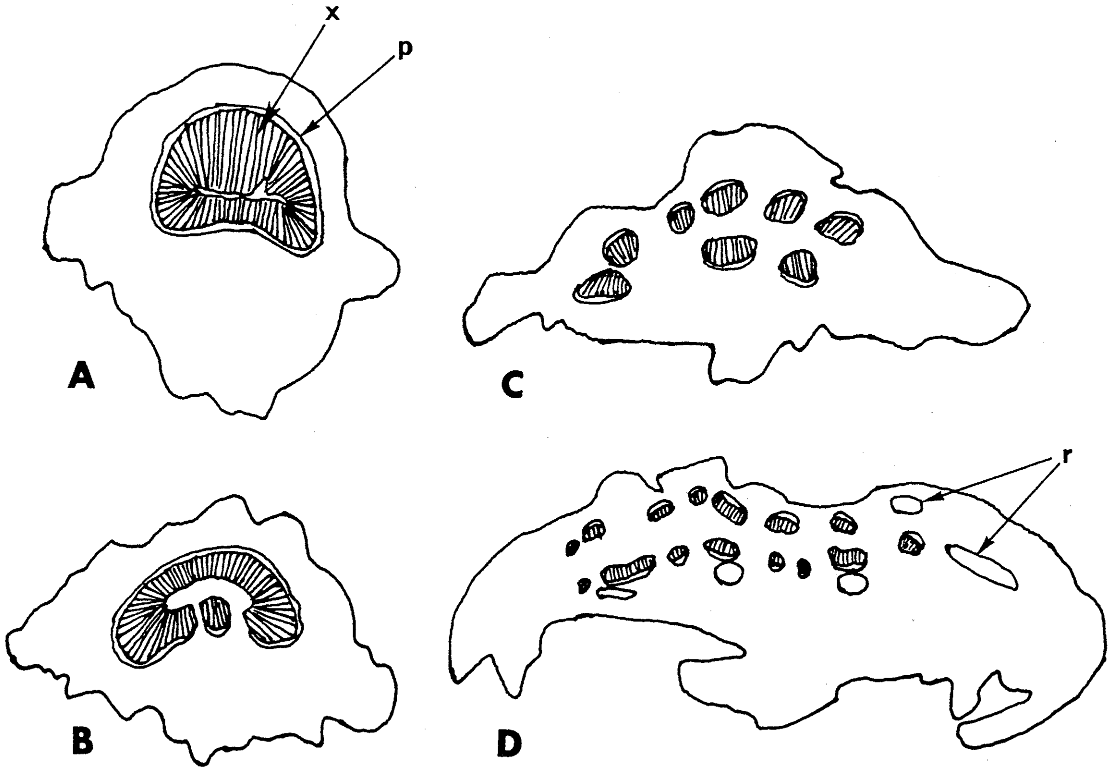

Fig. 26. Semi-diagrammatic figures of serial cross sections of bract-scale complex of *Sequoia*-like cone showing arrangement of vascular bundles and resin canals. p: phloem, r: resin canal, x: xylem.

abaxially concave reniform vascular cylinder to bract-scale complex instead of an elliptical vascular cylinder. The specimen resembles *Metasequoia* in this respect.

Three taxodiaceous genera of *Sequoia*-like seed cones, *Austrosequoia, Nephrostrobus,* and *Haborosequoia,* have been reported from the Cretaceous worldwide. *Haborosequoia* from Hokkaido (in the previous part of this paper) differs from the present specimen in size and the arrangement of resin canals, and in lacking a horizontal groove on the distal surface of cuneately peltate bract-scale complex. As discussed previously *Nephrostrobus* has a unique adaxially concave vascular-strand arrangement in the complex. *Austrosequoia* resembles this specimen in having peltate bract-scale complexes with a horizontal groove on distal surface (Peter and Christophel 1978; Tab. 1). However, the precise vasculature of the bract-scale complex of *Austrosequoia* was not described, so we cannot compare this specimen exactly with *Austrosequoia.* The newly described cone may be a new genus with a combination of *Sequoia, Sequoiadendron* and *Metasequoia* features and exhibiting close affinities with them.

Figs. 19–25. *Sequoia*-like cone. 19. Longitudinal section of cone. Bar 5 mm. 20. Cross section of base of bract-scale complex showing abaxially concave reniform and cylindrical vascular strand. Bar 0.5 mm. 21. Cross section of distal part of bract-scale complex showing fundamental tissues and vascular bundles arranged in two rows. Bar 0.2 mm. 22. Longitudinal section of bract-scale complex showing horizontal groove on distal surface of complex (arrow). 23, 24. Serial cross section of middle part of bract-scale complex showing arrangement of vascular bundles. Bars 0.5 mm. 25. Cross section of distal part of bract-scale complex showing arrangement of vascular bundles. Bar 1 mm.

Discussion

The present *Sequoia*-like cone and *Austrosequoia* are very similar to *Sequoia* and *Sequoiadendron,* which means that the *Sequoia* and *Sequoiadendron* forms had already appeared by the late Cretaceous. Their morphologies remain in the Recent with only minor changes. On the other hand, some specialized forms such as *Nephrostrobus,* which exhibits adaxially concaved arrangement of vascular bundles, and *Haborosequoia,* which exhibits wide and numerous resin canals in the bract-scale complex and completely fused bract and scale that is not distinguishable externally, were also present in the late Cretaceous. It is interesting that the cones that exhibits more specialized features than extant genera existed in the Cretaceous. Fossil records of *Sequoia*-like allies indicate that they were more diverse in the late Cretaceous than the Recent.

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要 旨

北海道上部白亜系から産出した，*Sequoia* と類似した果鱗複合体の外形及び維管束系を持った球果化石を2種類報告する．羽幌町から中島勇氏が採集した球果は，卵形で最大径15㎜に達する．種鱗と包鱗の維管束はスギ科現生の *Sequoia, Metasequoia, Sequoiadendron* と類似しており，球果軸の中心柱からひとつのリングとして現れるが，後にほぼ同じ位の数の向軸側の種鱗維管束列と背軸側の苞鱗維管束列に別れる．しかし維管束列の背軸側に極めて大きくたくさんの樹脂道が発達する点が特徴的であり，新属を立て，*Haborosequoia nakajimae* と命名した．

小平町から嶋貫年男氏が採集した球果は，最大径17㎜で保存は良くないが *Sequoia, Sequoiadendron* と極めてよく類似しており，現生属とほとんど変わらない形態を持った球果が白亜紀に存在したことを示唆した．これらを含め白亜紀の *Sequoia* 様球果はかなり多型であったと思われる．